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Originals

Achene Gross Morphology and Pericarp Anatomy of Japanese *Bolboschoenus* (Cyperaceae)

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Achene shapes and pericarp sections of the Japanese species of *Bolboschoenus* (Asch.) Palla, i. e., *B. fluviatilis* (Torr.) Soják subsp. *yagara* (Ohwi) T.Koyama, *B. maritimus* (L.) Palla, and *B. planiculmis* (F.Schmidt) T.V.Egorova, are described and illustrated with optical and scanning electron micrographs. Taxonomic significance is recognized in achene shape and color, number and persistence vs. caducity of perianth segments, shape and size of exocarp cells, presence vs. absence of silica bodies in lumina of exocarp cells, thickness of mesocarp, arrangement and cell wall thickness of mesocarp fibers, and thickness of endocarp. Two types of achenes are recognized within the Japanese plants so far known as *B. fluviatilis* subsp. *yagara* by their shapes and the structure of exocarp and mesocarp. A key to the Japanese species of *Bolboschoenus* is provided based on achene and pericarp characters in addition to those so far used. Distinctions and relationships are discussed for the Japanese species.

Key words: achene gross morphology, *Bolboschoenus*, Cyperaceae, pericarp anatomy, taxonomy.

Bolboschoenus (Asch.) Palla, one of the segregates of *Scirpus* L. s. lat. with about 16 species distributed worldwide (Goetghebeur and Simpson 1991), has been treated as a distinct genus in recent floras (Adams 1994, Hooper 1985, Koyama et al. 2000, Kozhevnikov 1988, Simpson and Koyama 1998). A few authors include the genus in *Schoenoplectus* (Rchb.) Palla (Strong 1993, 1994, Lye 1971, 1995), from which, however, *Bolboschoenus* differs in glumes pubescent over their entire surfaces and comparatively large achene epidermal cells (Koyama 1980, Marek 1958). Other characters such as presence of corms at culm bases, presence of more than one nodes on a culm above base, leaf-like involucral bracts, and ligule absence are also frequently used to distinguish *Bolboschoenus* from *Schoenoplectus*, but both genera include a few species with exceptional morphology for these characters. Eastern Asian *B. planiculmis* (F.Schmidt) T.V.Egorova lacks both prominent corms at culm bases and nodes on a culm above base, and has culm-like involucral bracts, as commonly observed in *Schoenoplectus*. Some *Schoenoplectus* species without leaf blades, e. g., *S. mucronatus* (L.) Palla, lack ligules as in *Bolboschoenus*. Strict definition of both genera, therefore, awaits further study.

Species delimitations within *Bolboschoenus* have been much confused because of large morphological variation, as is remarkable in widespread *B. maritimus* (L.) Palla (Krahulec et al. 1996, Norlindh 1972). A revision of the genus is needed to clarify the distinctions of species and their relationships (Goetghebeur 1998, Wilson 1981).

Cyperaceous species share much reduced organizations with rather few characters of taxonomic value. In addition to gross morphological ones, therefore, micromorphological or anatomical characters have been used for the taxonomy of the family. The internal structures of leaf blades and other vegetative organs were extensively studied (Bruhl 1995, Koyama 1966, 1967, Metcalfe 1969, 1971), but the reproductive ones have rarely been used until recently except for embryo forms (Van der Veken 1965) and structure of achene epidermal cells in various genera (Denton 1983: *Cyperus* L., Menapace 1993: *Eleocharis* R.Br., Rettig 1990: *Carex* L., Schuyler 1971: *Scirpus* s. lat., Tucker and Miller 1990: *Eriophorum* L.).

Achene structure of *Bolboschoenus* is recently paid attention to and its taxonomic significance was evaluated. Kowal (1958) and Marek (1958) provided line drawings of achenes and pericarp sections of 17 species of *Scirpus* s. lat. including *B. maritimus*, pointing out considerable variations within *Scirpus* s. lat. Oteng-Yeboah (1974), on the basis of achene characters alone, recognized two sections within *Bolboschoenus*, i. e., sect. Bolboschoenus and sect. Lentischoenus Oteng-Yeb. In his key to the sections, Oteng-Yeboah used the number of style branches, shape of achenes, and shape of exocarp cells, whose observations were extended to the recent studies with scanning electron microscopy for species represented in Africa (Browning and Gordon-Gray 1992, 1993, Browning et al. 1998a, b), North America (Browning et al. 1995), Europe (Browning et al. 1996, 1997b), and Australia and New Zealand (Browning et al. 1997a). They revealed the anatomical characters of achenes of *Bolboschoenus* useful in clarifying the species limits and in detecting natural hybridization, which are difficult if based only on the gross morpholoy.

Browning and Gordon-Gray (1993) and Browning et al. (1998a), based on achene and embryo characters, proved that the plants so far known as *Bolboschoenus maritimus* in the area of the Flora of southern Africa consist of two species, i. e., *B. maritimus* and *B. glaucus* (Lam.) S.G.Smith. They also reported the occurrence of eastern Asian *B. yagara* (Ohwi) Y.C.Yang & M.Zhan [= *B. fluviatilis* (Torr.) Soják subsp. *yagara* (Ohwi) T.Koyama] in Europe, where only *B. maritimus* had previously been recorded (Browning et al. 1996). Evidence of natural hybridization within the genus, which is supposedly increasing the difficulties in species delimitations, was detected by Browning et al. (1995, 1996) based mostly on the intermediate structure of the achenes and persistence of the perianth segments on the shed achenes. These studies should be extended to all species worldwide to provide a broad comparison of pericarp structure within the genus (Browning et al. 1995).

Three species of *Bolboschoenus*, i. e., *B. fluviatilis* subsp. *yagara*, *B. maritimus*, and *B. planiculmis*, are so far known from Japan (Koyama 1980). The present paper illustrates achene shapes and pericarp sections of the Japanese species of the genus with optical and scanning electron micrographs, and discusses the species distinctions and their relationships.

Materials and Methods

Mature achenes were extracted from herbarium specimens deposited in TUS and TUSG, which were identified by Hayasaka. Three achenes from each specimen were observed and their length including beak and maximum width were measured under dissecting microscope. The achenes for optical and scanning electron micrographs were extracted from representative specimens indicated by "[OM]" and "[SEM]" respectively in the lists of voucher specimens for each species. Optical micrographs of abaxial faces of achenes were taken with the binoculars Leica MZ12. The achenes were then sub-

merged in liquid nitrogen, hand-sectioned transversely or longitudinally with surgical knife at a point mid-way of achene length or width. The sections, seeds removed, were mounted on metal stubs, platinum-palladium coated with Hitachi E-1030 ion-sputter and then osmium coated with Nippon Laser & Electronics Lab. NL-OPC80A ion-sputter, photographed with Hitachi S-4100 scanning electron microscope at 2.0–4.0 kV.

Results

1. General features of achene structure of *Bolboschoenus*

Achenes of *Bolboschoenus* observed are obovate with conical beak on the tip (Figs. 1a, 2a, 4a, 5a), trigonous or dorsiventrally compressed in transverse sections (Figs. 1b, 2b, 2c, 4b, 5b), light- to blackish brown when ripe. Perianth segments attached to the base of achenes are retrorsely barbed, persistent (Fig. 1a) or caducous (Fig. 2a). Achene epidermal cells are pentagonal to heptagonal, isodiametric or slightly elongated longitudinally in the surface view (Fig. 3d). Pericarps are consisted of sclerenchyma cells, in which exocarp (achene epidermis), mesocarp, and endocarp are distinguished in transverse or longitudinal sections (Figs. 1d, 1e, 2d, 2e, 3b, 4d, 4e, 5c, 6). Exocarps are one layer of thick-walled, prismatic sclerenchyma cells, in the lumina of which silica bodies are present (Fig. 1c, arrow) or absent (Figs. 2d, 2e, 4d, 4e, 5c). Exocarp cells are ca. isodiametric (Fig. 1c) or radially elongated (Figs. 2d, 2e, 4d, 4e, 5c), deeper at the cor-

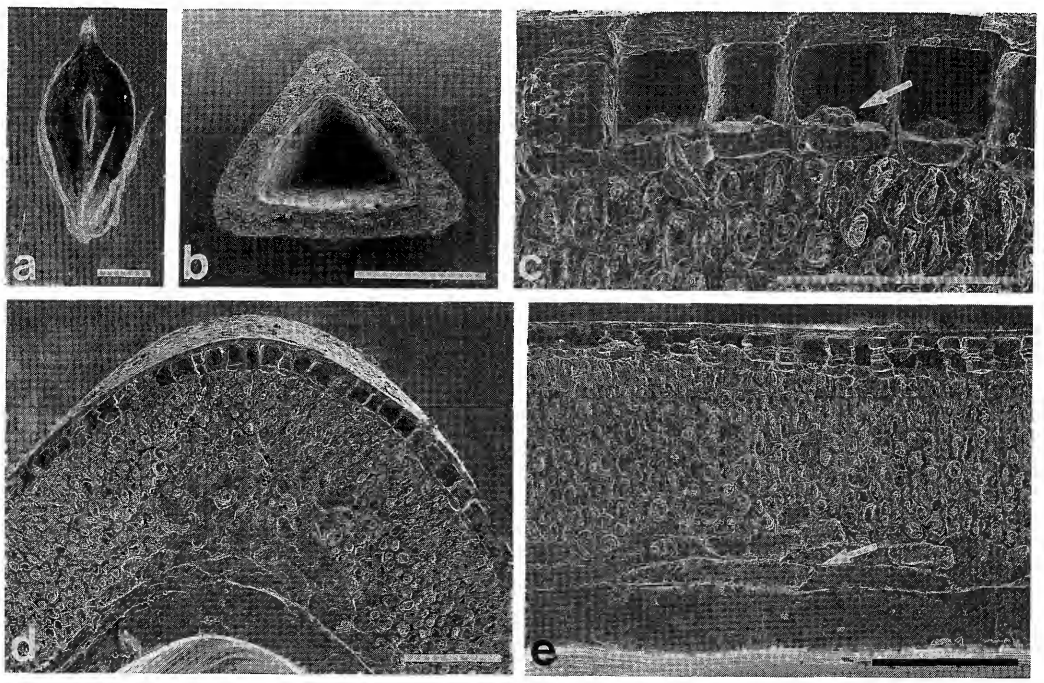

Fig. 1. Achenes of *Bolboschoenus fluviatilis* subsp. *yagara*, type A (a, c–e: E. Hayasaka 970902141, TUS; b: E. Hayasaka 2211, TUS). a. Outline. b–e. Transverse sections (b: outline; c: exocarp cells with silica bodies in lumina [arrow] and outer part of mesocarp; d: corner of achene; e: abaxial face, transversely elongated fibers in inner part of mesocarp [arrow]). Scale bars: a, b = 1 mm; c = 50 μm; d, e = 100 μm.

ners of achenes than at the abaxial and adaxial faces in transverse sections (Figs. 2b–e, 4b, 4d, 4e), or regularly deep throughout the whole part of achenes (Figs. 1b, 1d, 1e, 5b). Anticlinal walls of the exocarp cells are straight (Fig. 1c) or wavy (Figs. 2d, 2e), and outer periclinal walls are thicker than inner periclinal walls (Fig. 4e). Mesocarps are 4–13 layers of solid or hollow fibers longitudinally elongated (Figs. 1c, 2d), and transversely elongated fibers are sometimes present in the innermost two or three layers (Fig. 1e, arrow). The outermost layer of mesocarp fibers are often distinguished from the inner layers by their smaller diameter and thicker walls (Figs. 3a, arrow, 6a). Vascular bundles with thin-walled, narrower cells are observed in mesocarps at the corners of achenes in transverse sections (Fig. 4c, arrow). Spiral thickenings and pits of mesocarp fibers are observed in longitudinal sections (Fig. 3c). Endocarps are one layer of thick-walled fibers transversely elongated, ca. square in longitudinal sections (Figs. 3b, 6b).

2. Description for each species

Bolboschoenus fluviatilis (Torr.) Soják subsp. **yagara** (Ohwi) T.Koyama

Two types of achenes are recognized within the Japanese plants so far known as *Bolboschoenus fluviatilis* subsp. *yagara*. We here tentatively call them type A and type B.

Type A (Fig. 1)

Achenes (Fig. 1a) narrowly obovate, 3.0–4.2 mm long, 1.4–2.8 mm wide, blackish brown when ripe. Beaks ca. 0.6 mm long, ca. 0.5 mm wide at base. Perianth segments 6, × 0.4–0.9 of achene length, persistent.

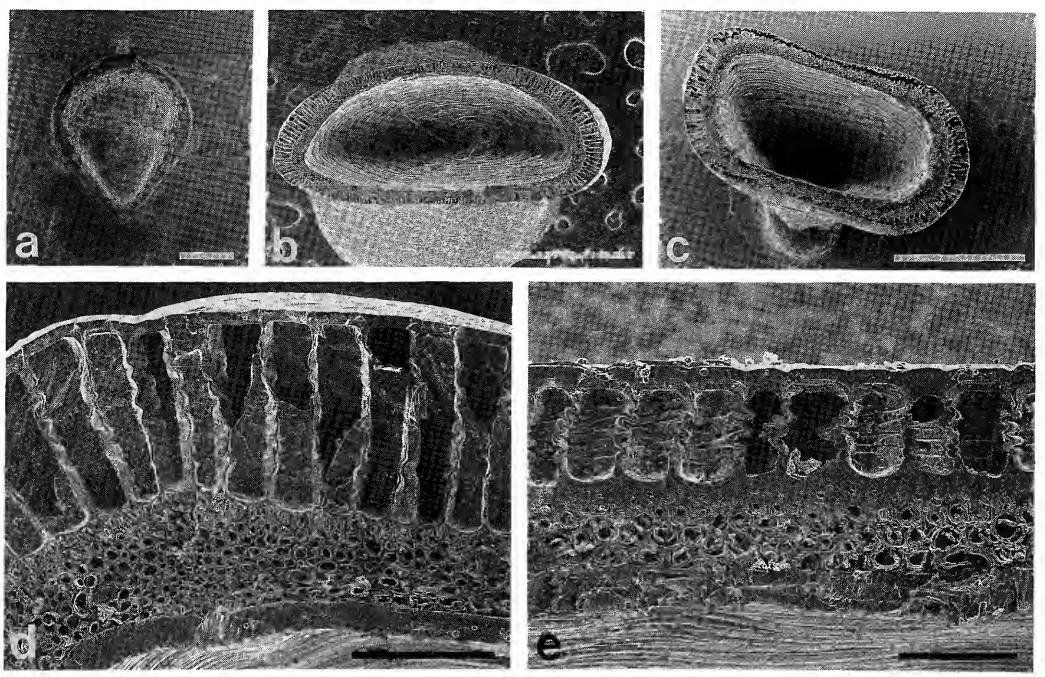

Fig. 2. Achenes of *Bolboschoenus maritimus* (a, b, d, e: K. Hosoi s. n., TUS; c: E. Hayasaka 2830, TUS). a. Outline. b–e. Transverse sections (b, c: outline; d: corner of achene; e: abaxial face). Scale bars: a–c = 1 mm; d = 100 μm; e = 50 μm.

Achenes in transverse sections (Fig. 1b) equilaterally trigonous, corners sharp, abaxial and adaxial faces flat. Pericarp 200–300 μm thick, slightly thicker at the corners of achenes (Figs. 1d, 1e). Exocarp 10–34 μm thick. Exocarp cells (Fig. 1c) almost square in transverse sections, regularly 10–34 μm deep throughout the whole part of achenes, 20–25 μm wide, round silica bodies present in lumina arising from inner periclinal walls, anticlinal walls straight or slightly wavy. Mesocarp 150–220 μm thick, with 10–12 layers of fibers, slightly thicker at the corners of achenes. Mesocarp fibers (Figs. 1d, 1e) mostly solid, 7.8–13 μm in diameter, longitudinally elongated in outer ca. 10 layers, transversely elongated in inner 2–3 layers. Endocarp (Figs. 1d, 1e) 40–43 μm thick.

Voucher specimens: JAPAN. Miyagi Pref.: Shiroishi City, Fukuoka, Noma, alt. ca. 300 m, 7 Sep. 1980, M. Usuba 10702 (TUS); Shiroishi-shi, Otakazawa-omachi, Benten-numa, alt. 110 m, 2 Sep. 1997, E. Hayasaka 970902141 (TUS) [OM, SEM]; Tome-gun, Hasama-cho, Kitakata, Lake Naganuma, alt. 10 m, 24 Jul. 1998, E. Hayasaka 2211 (TUS) [SEM]. **Fukushima Pref.**: Fukushima City, Tsuchiyu, Menuma Pond, alt. ca. 500 m, 19 Aug. 1975, M. Usuba 4500 (TUS); Kawanuma-gun, Aidzu-bange Town, Tabanematsu, Shimonuma Pond, alt. ca. 260 m, 21 Sep. 1980, M. Usuba 10730 (TUS); Soma City, Ishikami, Pond Ebisawa-ike, alt. 40 m, 1 Aug. 1998, E. Hayasaka 2324 (TUS). **Nagano Pref.**: Ueda-shi, Lake Sugawa-ko, alt. 680–700 m, 29 Jul. 1996, T. Ikeda s. n. (TUS).

Type B (Fig. 5)

Achenes (Fig. 5a) obovate, 3.4–4.4 mm long, 2.1–2.8 mm wide, blackish brown when ripe. Beaks ca. 0.5 mm long, ca. 0.5 mm wide at base. Perianth segments 3–6, × 0.4–0.8 of achene length, persistent. Achenes in transverse sections (Fig. 5b) compressed trigonous, corners round, abaxial and adaxial faces concave. Pericarp 220–330 μm thick, slightly thicker at the corners of achenes (Figs. 5b, 5c). Exocarp 45–74 μm thick. Exocarp cells (Fig. 5c) radially elongated, regularly 45–74 μm deep throughout the whole part of achenes, 20–30 μm wide, silica bodies absent in lumina, anticlinal walls prominently wavy. Mesocarp 150–220 μm thick, with 10–13 layers of fibers, slightly thicker at the corners of achenes. Mesocarp fibers (Fig. 5c) mostly solid, 7.5–11 μm in diameter, longitudinally elongated. Endocarp (Fig. 5c) 30–45 μm thick.

Voucher specimens: JAPAN. Aomori Pref.: Kamikita County, Rokkasho Village, Obuchi, Lake Obuchinuma, alt. 0 m, 18 Aug. 1999, E. Hayasaka 2822 (TUS) [OM, SEM]; Ogawara Lake, Takase River, 29 Jul. 1964, H. Ohashi 4021 (TUS); Kamikita-gun, Rokkasho-mura, the mouth of the River Takase, 10 Aug. 1973, T. Naito et al. s. n. (TUSG). **Niigata Pref.**: Joetsu-shi, Oritahama, 18 Aug. 1939, J. Yoshikawa s. n. (TUS); Kariwa County, Nishiyama Town, Osaki, alt. 1 m, 11 Aug. 1983, I. Ito 25108 (TUS). **Fukuoka Pref.**: Munakata-gun, Genkai-machi, Eguchi, around O-ike Pond, alt. 10-20 m, 12 Jul. 1984, S. Watanabe s. n. (TUS).

Bolboschoenus maritimus (L.) Palla (Figs. 2, 3)

Achenes (Fig. 2a) broadly obovate, 2.9–4.2 mm long, 2.0–2.6 mm wide, light- to dark brown when ripe. Beaks short, ca. 0.2 mm long, ca. 0.25 mm wide at base. Perianth segments 2–4, caducous. Achenes in transverse sections (Figs. 2b, 2c) plano-convex, plano-concave, or biconcave. Pericarp 100–290 μm thick, much thicker at the corners of achenes (Figs. 2b-e). Exocarp 45–140 μm thick. Exocarp cells (Figs. 2d, 2e) radially elongated, 45–55 μm deep at the abaxial and adaxial faces, 120–140 μm deep at the corners of achenes, 20–40 μm wide, silica bodies absent in lumina, anticlinal walls prominently wavy. Mesocarp 34–130 μm thick, with 4–11 layers of fibers, thicker at the corners of achenes. Mesocarp fibers (Figs. 2d, 2e, 3a-c) solid in the outermost one layer, mostly hollow in inner layers, 4–16 μm in diameter, longitudinally elongated. Endocarp (Figs. 2d, 3b) ca. 20 μm thick.

Voucher specimens: JAPAN. Hokkaido Pref.: Abashiri Division, Abashiri-shi, Lake Notoro-ko, 3 Sep. 1963, A. Matsumoto 38-10 (TUS). **Aomori Pref.**:

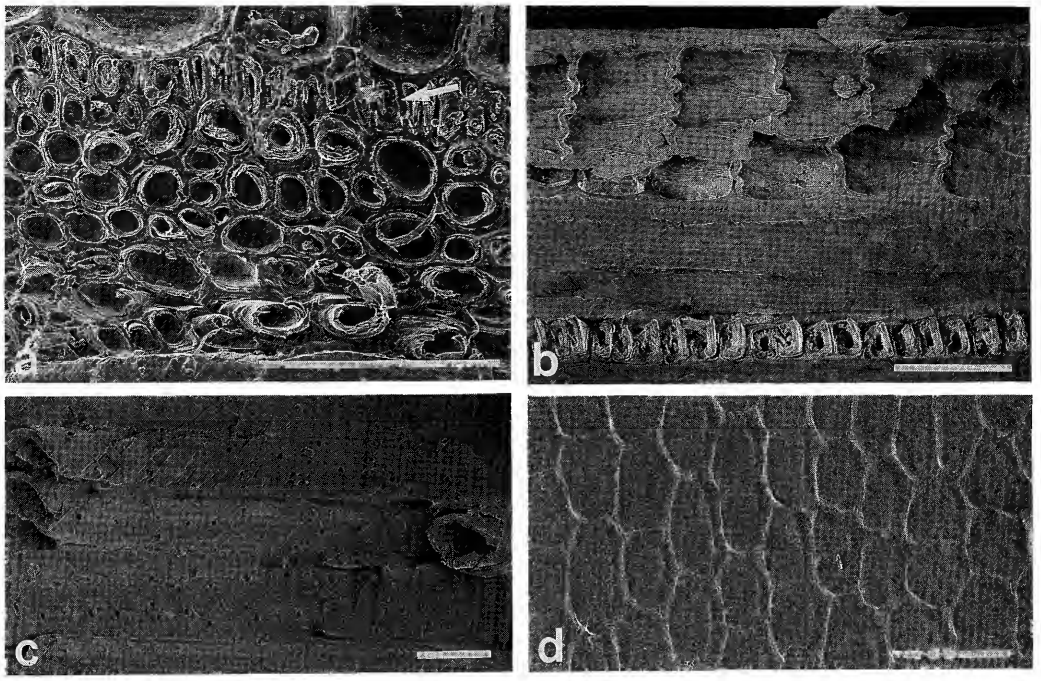

Fig. 3. Achenes of *Bolboschoenus maritimus* (K. Hosoi s. n., TUS). a. Transverse section showing mesocarp, thin and solid fibers in the outermost layer [arrow]. b, c. Longitudinal sections (b: abaxial face; c: mesocarp fibers). d. Outer surface. Scale bars: a, b, d = 50 μm; c = 10 μm.

Nishitsugaru-gun, Kitakanagasaki, 31 Jul. 1957, K. Hosoi s. n. (TUS) [OM, SEM]; Kamikita County, Rokkasho Village, Obuchi, Lake Obuchinuma, alt. 0 m, 18 Aug. 1999, E. Hayasaka 2830 (TUS) [SEM]. **Miyagi Pref.**: Yamamoto-cho, Sakamoto, 18 Jul. 1979, K. Shoji s. n. (TUS); Watari-gun, Yamamoto-cho, Ushibashi-kakoh, alt. 0 m, 1 Sep. 1992, T. Mori 8024 (TUS). **Niigata Pref.**: Isl. Sado, Sado-gun, Ogi-machi, Mitsuya, 22 Jul. 1954, J. Yoshikawa 2290 (TUS); Kariwa-gun, Nishiyama-machi, Ishiji, Osaki, 11 Aug. 1952, J. Yoshikawa 696 (TUS). **Chiba Pref.**: Chosei-gun, Shirako-machi, Seki, 21 Jul. 1971, S. Suzuki s. n. (TUS). **Hyogo Pref.**: Himeji-shi, 11 Jun. 1991, M. Yanai 10849 (TUS).

Bolboschoenus planiculmis (F.Schmidt) T.V.Egorova (Fig. 4)

Achenes (Fig. 4a) broadly obovate, 3.2–4.0 mm long, 2.2–2.4 mm wide, light- to dark brown when ripe. Beaks short, ca. 0.2 mm long, ca. 0.3 mm wide at base. Perianth segments 6–7, ca. × 0.6 of achene length, caducous. Achenes in transverse sections (Fig. 4b) biconvex or plano-convex. Pericarp 100–200 μm thick, much thicker at the corners of achenes (Figs. 4b, 4d, 4e). Exocarp 55–140 μm thick. Exocarp cells (Figs. 4d, 4e) radially elongated, ca. 55 μm deep at the abaxial and adaxial faces, 98-140 μm deep at the corners of achenes, 25–37 μm wide, silica bodies absent in lumina, anticlinal walls straight or slightly wavy. Mesocarp 25–80 μm thick, with 4–7 layers of fibers, thicker at the corners of achenes. Mesocarp fibers (Figs. 4c-e) hollow, 5.5–20 μm in diameter, longitudinally elongated. Endocarp (Fig. 4e) ca. 20 μm thick.

Voucher specimens: JAPAN. Aomori Pref.: Kamikita County, Rokkasho Village, Obuchi, Lake Obuchinuma, alt. 0 m, 3 Oct. 1999, E. Hayasaka 2910

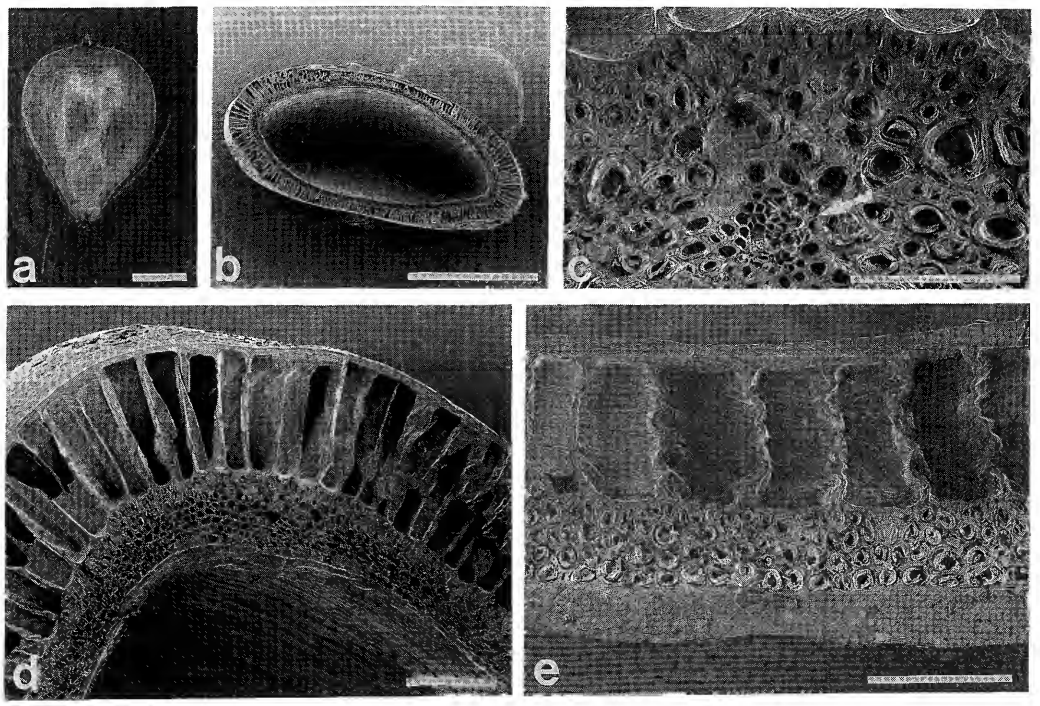

Fig. 4. Achenes of *Bolboschoenus planiculmis* (a, b, d: E. Hayasaka 2910, TUS; c, e: C. Suzuki s. n., TUS). a. Outline. b–e. Transverse sections (b: outline; c: mesocarp, vascular bundle with thin-walled cells [arrow]; d: corner of achene; e: abaxial face). Scale bars: a, b = 1 mm; c, e = 50 μm; d = 100 μm.

(TUS) [OM, SEM]. **Fukushima Pref.**: Iwaki-shi, the lower course of the Same River, alt. ca. 0 m, 16 Sep. 1985, M. Usuba s. n. (TUS). **Chiba Pref.**: Sanbu-gun, Hitotsumatsu-mura, 15 Jul. 1939, C. Suzuki s. n. (TUS) [SEM]; Chosei-gun, Ichinomiya-machi, 15 Jul. 1934, C. Suzuki s. n. (TUS).

Discussion

Taxonomic significance of achene structure in *Bolboschoenus*

Close examinations in pericarp structure of *Bolboschoenus* in the present paper, in Marek (1958), and in a series of studies by Browning et al. all show that the species of the genus share thick pericarps with large, prismatic exocarp cells often radially elongated. In *Schoenoplectus*, however, exocarp cells are smaller and shallower in transverse sections (Hayasaka unpublished data). A close comparison of pericarp structure between *Bolboschoenus* and *Schoenoplectus* is needed, which we think will provide useful information about the distinctions between the two genera.

Interspecific variations are observed in achene shape and color, number and persistence vs. caducity of perianth segments, shape and size of exocarp cells, presence vs. absence of silica bodies in lumina of exocarp cells, thickness of mesocarp, arrangement and cell wall thickness of mesocarp fibers, and thickness of endocarp in Japanese *Bolboschoenus*. Our preparatory observations have confirmed that these characters are mostly stable within species, and thus serve as additional criteria to the characters hitherto used for delimiting species in the genus. Koyama (1980) provided a key to the Japanese species of *Bolboschoenus* based on

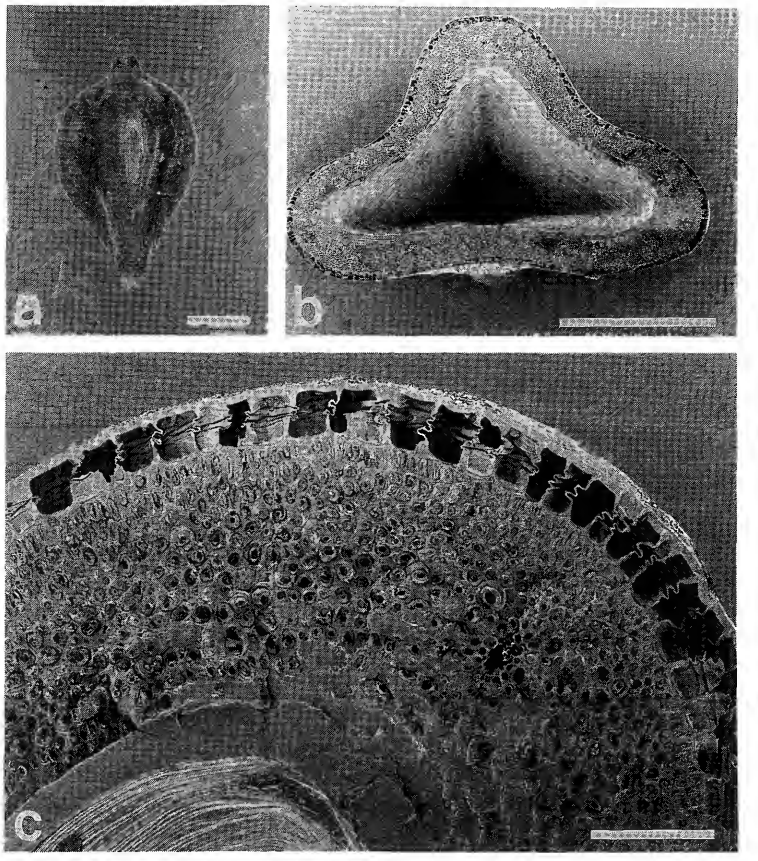

Fig. 5. Achenes of *Bolboschoenus fluviatilis* subsp. *yagara*, type B (E. Hayasaka 2822, TUS). a. Outline. b, c. Transverse sections (b: outline; c: corner of achene). Scale bars: a, b = 1 mm; c = 100 μm.

characters of achenes, inflorescences, leaf blades, style branches, perianth segments, and spikelets. Of these characters, shape of inflorescences and number of spikelets per inflorescence are often variable within species, correlated with growing conditions and inter-clonal difference in genetic backgrounds (Browning and Gordon-Gray 1999, Krahulec et al. 1996). We here provide a key to the Japanese species of the genus based on achene and pericarp characters in addition to those used by Koyama (1980) and other cyperologists, which summarizes the results of the present paper.

Key to the Japanese species of *Bolboschoenus*

1. Styles trifid; perianth segments persistent; achenes trigonous, blackish brown when ripe; exocarp cells regularly deep throughout the whole part of achenes; mesocarp fibers mostly solid; endocarps more than 30 μm thick; inflorescences with several to more than 20 spikelets.....2
1. Styles bifid; perianth segments caducous; achenes lenticular, light- to dark brown when ripe; exocarp cells deeper at the corners of achenes than at the abaxial and adaxial faces; mesocarp fibers mostly hollow; endocarps

ca. 20 μm thick; inflorescences with 1 to several spikelets 3

2. Achenes narrowly obovate, equilaterally trigonous, corners sharp, abaxial and adaxial faces flat in transverse sections; exocarp cells ca. isodiametric, less than 34 μm deep, silica bodies present in lumina; mesocarp fibers longitudinally elongated in outer layers, transversely elongated in inner layers ..... *B. fluviatilis* subsp. *yagara* with type A achenes

2. Achenes obovate, compressed trigonous, corners round, abaxial and adaxial faces concave in transverse sections; exocarp cells radially elongated, more than 45 μm deep, silica bodies absent in lumina; mesocarp fibers longitudinally elongated ..... *B. fluviatilis* subsp. *yagara* with type B achenes

3. Perianth segments 2–4; achenes convex or concave; mesocarps up to 130 μm thick; leaf blades and involucral bracts V-shaped in transverse sections; culms noded above base; creeping rhizomes hard; corms at culm-bases well-developed; spikelets several ..... *B. maritimus*

3. Perianth segments 6–7; achenes convex; mesocarps up to 80 μm thick; leaf blades and involucral bracts trigonous in transverse sections; culms nodeless above base; creeping rhizomes flaccid; corms at culm-bases apparently absent; spikelets 1–3..... *B. planiculmis*

Bolboschoenus fluviatilis subsp. **yagara**

According to the original description of *Scirpus yagara* Ohwi (Ohwi 1944) and the illustrations in Koyama (1958), achenes of *Bolboschoenus fluviatilis* subsp. *yagara* are equilaterally trigonous, which agree with the type A achenes. Thus plants with the type A achenes are here considered typical *B. fluviatilis* subsp. *yagara*, and those with the type B achenes need further study.

Bolboschoenus fluviatilis subsp. *fluviatilis* is distributed in North America and subsp. *yagara* (Fig. 7) is in Japan, Russian Far East, China, Korea, and Europe. The latter is distinguished from the former by smaller habit

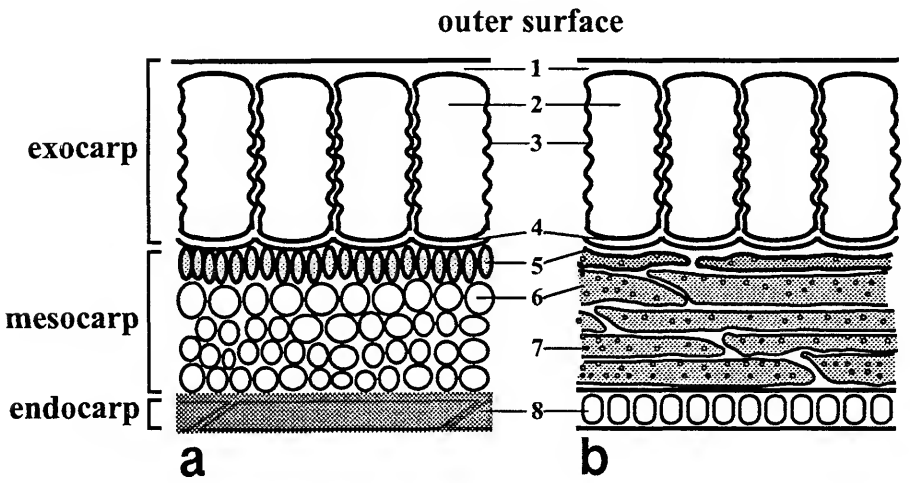

Fig. 6. Schematic drawings illustrating representative structure of pericarp (drawn from *Bolboschoenus maritimus* achenes). a. Transverse section. b. Longitudinal section. 1. outer periclinal wall of exocarp cell; 2. lumen of exocarp cell; 3. anticlinal wall of exocarp cell; 4. inner periclinal wall of exocarp cell; 5. mesocarp fiber in the outermost layer; 6. mesocarp fiber in the inner layer; 7. pit of mesocarp fiber; 8. endocarp fiber.

and achenes (Koyama 1980). Koyama (1958) provided achene measurements as 4.0–5.0 × 2.3–2.5 mm for subsp. *fluviatilis* and 3.5–4.0 × 1.8 mm for subsp. *yagara*, and so did Koyama (1980) as 3.8–4.2 × 2.0–2.5 mm and 2.5–3.5 × 1.8–2.2 mm respectively. But it is not clear whether or not both of Koyama's measurements of achene length included beak. Browning et al. (1995) provided achene measurements for North American subsp. *fluviatilis* as 3.8–5.5 × 2.0–2.9 mm including beak, and so did we 3.0–4.2 × 1.4–2.8 mm for Japanese subsp. *yagara* (type A), which confirm that the latter has smaller achenes than the former. But the achenes of the species from Australia and New Zealand (Browning et al. 1997a), and Russian Far East (Kozhevnikov 1998) have intermediate size between the two subspecies, which obscure the distinction between the two by achene size.

Achenes of *Bolboschoenus fluviatilis* subsp. *fluviatilis* (Browning et al. 1995, Browning and Gordon-Gray 2000) and those of subsp. *yagara* (Fig. 1) are equilaterally trigonous, with exocarp cells which are almost isodiametrically shaped and have silica bodies in lumina. They are similar to each other and readily distinguishable from those of other species. Our present observation does not support the specific segregation of subsp. *yagara* from *B. fluviatilis* though some authors treat it as a distinct species (Browning et al. 1996, Kozhevnikov 1988, Zhan and Yang 1987). But an observation of achenes removed from the type specimen of *Scirpus yagara* is needed to confirm its taxonomic status, as has done for Australian and New Zealand species (Browning et al. 1997a), together with more extensive sampling of achenes to cover the whole range of distribution of *B. fluviatilis*.

Plants with the type B achenes (Fig. 8) were found in scattered localities in Honshu and Kyushu, Japan. These have been referred to as *Bolboschoenus fluviatilis* subsp. *yagara* apparently because of trigonous, dark colored achenes. In addition to the difference in pericarp structure between typical *B. fluviatilis* subsp. *yagara* and plants with the type B achenes (Figs. 1, 5), the latter is somewhat smaller in plant size, and bears less numerous spikelets than the former. The radial elongation of exocarp cells of the type B achenes is intermediate between the type A and *B. maritimus* achenes. It is possible that plants with the type B achenes might be treated as a distinct species or natural hybrids between *B. fluviatilis* subsp. *yagara* and *B. maritimus* after a more detailed study. Evidence for natural hybridization between *B. fluviatilis* subsp. *yagara* and *B. maritimus* in regions of sympatry in Europe was presented by Browning et al. (1996, 1997b) and Hroudová et al. (1998). In North America, however, putative *B. fluviatilis* × *B. maritimus* hybrids are known only from a few collections from California even though these species are sympatric over large areas, and putative hybrids between *B. fluviatilis* × *B. robustus* (Pursh) Soják [= *B. novae-angliae* (Britt.) S.G.Smith] occur on the Atlantic coast where *B. maritimus* is also common (Browning et al. 1995, S. G. Smith pers. comm.). We have not confirmed in Japan whether or not *B. fluviatilis* subsp. *yagara* and *B. maritimus* are sympatric where plants with the type B achenes occur. Taxonomic status of the plants is not settled here pending further research.

Bolboschoenus maritimus

The Japanese plants of *Bolboschoenus maritimus* were previously known as *Scirpus maritimus* var. *compactus* (Hoffm.) Mayer (Miyabe and Kudo 1931) or *S. biconcavus* Ohwi (Ohwi 1944). Koyama (1980) reduced both *S. maritimus* var. *compactus* and *S. biconcavus* to *B. maritimus*, which he treated inclusively as a polymorphic species distrib-

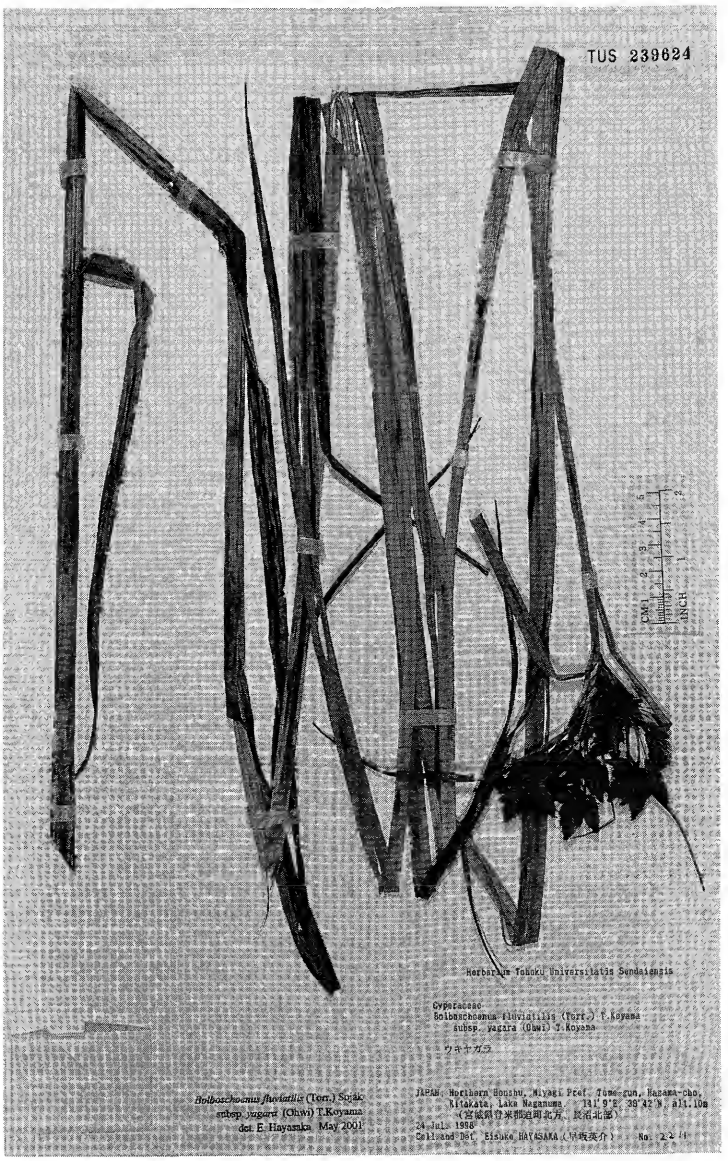

Fig. 7. *Bolboschoenus fluviatilis* subsp. *yagara* with type A achenes (E. Hayasaka 2211, TUS).

uted worldwide. Smith and Kukkonen (1999) designated a new lectotype for *S. maritimus* [Herb. Celsius **2**: 212 (UPS)] with an epitype carrying mature achenes [Sweden: E. Roslagen, par. Börstill, 2 km W. Kallö, near Husbacka, 14 Oct. 1995, Nilsson 9515 (UPS)], which supersede the lectotype formerly designated by Koyama (1962) which belongs to *B. robustus* of North America, and is in serious conflict with the protologue of *S. maritimus*.

Browning et al. (1996) provided scanning

Fig. 8. *Bolboschoenus fluviatilis* subsp. *yagara* with type B achenes (E. Hayasaka 2822, TUS).

electron micrographs of achenes removed from one of the iso-epitypes of *Scirpus maritimus*, which are trigonous with exocarp cells radially elongated. The Japanese plants of *Bolboschoenus maritimus* differ from *B. maritimus* s. str. in having lenticular achenes (Fig. 2). It is possible that the Japanese plants might be treated as a distinct species or a subspecies of *B. maritimus* after a more detailed study. A pericarp study of the type specimen of *S. biconcavus* is also needed.

Bolboschoenus planiculmis

Bolboschoenus planiculmis is a well-circumscribed eastern Asian endemic known from Russian Far East, the Pacific coast of Japan, China, and Taiwan (Koyama 1980, Koyama et al. 2000). The name *Scirpus planiculmis* F.Schmidt had long been misapplied to the eastern Asian plants of *S. maritimus* until Koyama (1980) correctly treated both species. *Bolboschoenus planiculmis* has trigonous leaf blades and trigonous, culm-like involucral bracts, flaccid rhizomes, and pseudolateral inflorescences with often solitary spikelet as illustrated by Shimizu (1967, *B. planiculmis* here as *Scirpus iseensis* T.Koyama & T.Shimizu, the name *S. planiculmis* misapplied to *S. maritimus*) and Koyama (1980). Roshevits (1935) confused the species with those of *Schoenoplectus* [= *Scirpus* sect. Schoenoplectus], apparently because of the superficial resemblance in vegetative morphology. Strong (1993, 1994) regarded *B. planiculmis* as one of the critical species intermediate between *Bolboschoenus* and *Schoenoplectus*.

The pericarp structure of *Bolboschoenus planiculmis* (Fig. 4) is similar to that of *B. maritimus* (Figs. 2, 3) as summarized in the first step of the key to the species above, which suggests the close relationship between the two species, giving no evidence that *B. planiculmis* is a intermediate species between *Bolboschoenus* and *Schoenoplectus*. *Bolboschoenus planiculmis* is highly aquatic, growing in tidal habitat where the plants are completely submerged when the tide is in (Shimizu 1967). The *Schoenoplectus*-like vegetative morphology of the species is here considered an adaptation to its tidal habitat and less important for delimiting genera. Flaccid habit of aquatic species is also known in *Schoenoplectus* sect. Malacogeton (Ohwi) S.G.Smith & Hayasaka (Smith and Hayasaka 2001).

Hroudová et al. (1997) suggested the relationship between fruit buoyancy and pericarp structure in *Bolboschoenus maritimus*. Pericarp of *B. planiculmis* has large air cavities in exocarp cells and relatively thin mesocarp layers (Fig. 4d) with high floating potential. We presume that the pericarp structure of the species is effective on seed dispersal in tidal habitat, as confirmed in *B. maritimus* subsp. *compactus* (Hoffm.) Hejný sampled from the seacoast of South Sweden (Hroudová et al. 1997).

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早坂英介，大橋広好：日本産ウキヤガラ属（カヤツリグサ科）の痩果の外部形態と果皮の内部構造

日本産ウキヤガラ属 *Bolboschoenus* (Asch.) Palla の3種すなわちウキヤガラ *B. fluviatilis* (Torr.) Soják subsp. *yagara* (Ohwi) T.Koyama，コウキヤガラ *B. maritimus* (L.) Palla，イセウキヤガラ *B. planiculmis* (F.Schmidt) T.V.Egorova の痩果の外部形態と果皮の断面構造を光学顕微鏡と走査型電子顕微鏡で観察，記載した．痩果の形と色，刺針状花被片の数とその宿存/早落性，外果皮の細胞の形と大きさ，外果皮の細胞内腔の珪酸体の有無，中果皮の厚さ，中果皮の繊維細胞の配列方向と細胞壁の厚さ，内果皮の厚さに種間で変異が見られ，これらの形質は日本産の種および亜種の分類に有効であることが明らかになった．痩果の形，外果皮と中果皮の構造の違いから，ウキヤガラとして知られていた植物の痩果には2つの型があることを見いだした．従来用いられてきた形質に痩果と果皮の形質を加えた日本産ウキヤガラ属の種への検索表を示し，種の区別と類縁を論じた．

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